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# The dynamics of the interrelation of perception and action across the life span

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Abstract

Successful social interaction relies on the interaction partners' perception, anticipation, and understanding of their respective actions. The perception of a particular action and the capability to produce this action share a common representational ground. So far, no study has explored the interrelation between action perception and production across the life span using the same tasks and the same measurement techniques. This study was designed to fill this gap. Participants between 3 and 80 years ($N = 214$) observed two multistep actions of different familiarity and then reproduced the according actions. Using eye tracking, we measured participants' action perception via their prediction of action goals during observation. To capture subtler perceptual processes, we additionally analysed the dynamics and recurrent patterns within participants' gaze behaviour. Action production was assessed via the accuracy of the participants' reproduction of the observed actions. No age-related differences were found for the perception of the familiar action, where participants of all ages could rely on previous experience. In the unfamiliar action, where participants had less experience, action goals were predicted more frequently with increasing age. The recurrence in participants' gaze behaviour was related to both, age and action production: Gaze behaviour was more recurrent (i.e. less flexible) in very young and very old participants, and lower levels of recurrence (i.e. greater flexibility) were related to higher scores in action production across participants. Incorporating a life-span perspective, this study illustrates the dynamic nature of developmental differences in the associations of action production with action perception.

*Key words:* Development; social cognition; dynamic systems; action production; common-coding; recurrence analyses

The dynamics of the interrelation of perception and action across the life span

Our society is built upon the interaction between its members. Successful social interaction relies on the interlocutors' reciprocal perception, anticipation, and understanding of others' behaviour that is often expressed through their observable goal-directed actions (Blakemore & Decety, 2001). Hence, the perception of others' actions (henceforth called *action perception*) serves as a foundation of the correct interpretation of their intentions as well as implicit and explicit goals (Gallese & Goldman, 1998). Furthermore, action perception facilitates joint action, cooperation, and social learning (Sebanz & Knoblich, 2009). Therefore, gaining knowledge on the factors influencing action perception is vital. Previous work indicates that action perception is affected by the interlocutors' capability to produce a specific action and vice versa (Hommel, Müsseler, Aschersleben, & Prinz, 2001). Furthermore, the accuracy and/or speed in performing a certain action (*action production*) along with action perception undergo substantial developmental changes across the whole life span (Adolph & Berger, 2011; Diersch, Cross, Stadler, Schütz-Bosbach, & Rieger, 2012; Gampe, Prinz, & Daum, 2015; Houx & Jolles, 1993). However, although evident, the age-related differences in the interrelations between action perception and action production have only been studied within narrow age ranges. Therefore, the aim of the current study was to determine how age-related variations in action production are interrelated with age-related differences in action perception across the human life span. Importantly, to allow for comparisons between the different age groups, action perception (via eye tracking) and action production (via imitation) were assessed with the same measurement techniques across all age groups.

Commonly, the interrelations between action perception and action production are assumed to be based on a common representational basis of perceived and produced actions (*common-coding approach*; Hommel et al., 2001). In support of this assumption, prior work has found evidence for overlapping cortical processing areas within the sensorimotor system for action perception and action production (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Grafton, 2009; Iacoboni et al., 1999; Léonard & Tremblay, 2008; Marty et al., 2015). In line with this sensorimotor dependency, previous studies indicate that the accumulated experience with actions (*motor experience*; Catmur, Walsh, & Heyes, 2009; Sommerville, Hildebrand, & Crane, 2008) and the observers' general motor competence (Wermelinger, Gampe, & Daum, 2017) influence the coupling of action perception and action production.

Developmental studies suggest that the coupling between action perception and action production skills emerges early in development (Meltzoff & Prinz, 2002). Already in 3-month-olds, motor experience with the to be observed action enhanced action perception and the infants were more likely to perceive the observed action as goal-directed (Sommerville, Woodward, & Needham, 2005). Similarly, infants' evaluation (Daum, Prinz, & Aschersleben, 2011) and anticipation (Ambrosini, Costantini, & Sinigaglia, 2011; Melzer, Prinz, & Daum, 2012) of the goal of a grasping action is correlated with their own action production skill. For instance, while simple reaching or feeding actions are anticipated already by 6-month-olds (Kochukhova & Gredebäck, 2010), only at the age of 12 months, infants anticipate the goal of more difficult reach-and-transport actions (Falck-Ytter, Gredebäck, & von Hofsten, 2006). On the neural level, the desynchronisation of the mu rhythm is shown to vary with toddlers' specific action production skill (Cannon et al., 2016; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). For instance, Cannon et al. (2016) showed a greater desychronisation during the perception of a grasping movement in 9- and 12-months-old's with better reach-and-grasping skills. The mu EEG rhythm is recorded over sensorimotor areas and its desynchronisation is associated with action perception and motor activity during action production (Pfurtscheller, Neuper, Flotzinger, & Pregenzer, 1997). Taken together, studies on infants show that action perception, independent of whether it is assessed through action evaluation, action prediction, or the activity of the sensorimotor system correlates with the children's skill to produce and experience with the respective action.

The interrelations between action perception and action production are not restricted to early stages of ontogenesis. On the behavioural level, adults with a particular motor expertise such as figure skating (Diersch et al., 2013) or tennis (Farrow & Abernethy, 2003) predict the continuation of an observed movement of their respective expertise more accurately than novices. Also in non-experts, action perception varies with action production skill: When observing video-recordings of their own actions (for which participants are expert performers) and recordings of other persons' actions, participants were more accurate in predicting the goal of their own actions (Knoblich & Flach, 2001; Knoblich, Seigerschmidt, Flach, & Prinz, 2002). Additionally, already short motor training in the respective action enhances the accuracy and speed of predicting the action goal (Hecht, Vogt, & Prinz, 2001; Möller, Zimmer, & Aschersleben, 2015). On the neural level, the activity of sensorimotor brain regions during action perception varies with the observers' experience with an action and action production skill (Catmur et al., 2008, 2009; Heyes, 2010; Press, Heyes, & Kilner, 2011). For example, brain areas involved in performing an action were engaged more strongly during the perception of actions for which the observers have a specific motor expertise than for actions for which the participants only possess visual experience (e.g. dancers: Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; volleyball and tennis players: Balser et al., 2014; pianists: Haslinger et al., 2005; Haueisen & Knösche, 2001; biologically possible vs. impossible actions: Stevens, Fonlupt, Shiffrar, & Decety, 2000).

In sum, the reviewed studies indicate that action perception and action production are related across the life span. However, when taking a life-span perspective, the specific form of the relationship may be expected to change over development. On the one hand, advancing age is assumed to go hand in hand with an accumulation of active motor experience with different actions. These differences in motor experience are associated with variations in the cortical representation of sensorimotor information (Karni et al., 1998; Matsuzaka, Picard, & Strick, 2007; Poldrack et al., 2005) and thereupon influence the perception of actions. In line with this, previous studies indicate the life-long differences in motor experience to be associated with according differences in action perception (Catmur et al., 2009; Sommerville et al., 2005). On the other hand, accuracy and speed in the production of particular actions (henceforth called *action production skills*) follow a more inverted U-shaped development: They increase across childhood (Adolph & Berger, 2011) and decrease again during adulthood (Houx & Jolles, 1993; Kauranen & Vanharanta, 1996). Early in life, in particular in infancy, increasing age is associated with enhanced prospective action control (von Hofsten & Rönnqvist, 1988) and increased accuracy of goal-directed movements (D'Souza, Cowie, Karmiloff-Smith, & Bremner, 2017; von Hofsten, 2004). Towards the upper end of the life span, in late adulthood, advancing age is characterised by less precise motor planning (Reuter, Behrens, & Zschorlich, 2015) and reduced sensorimotor control of actions (Seidler & Stelmach, 1995). Importantly, because of their common base, these differences in action production skills across the life span are associated with according differences in action perception. That is, paralleling the increase and decline of action production skill, the prediction of an action goal increases in early childhood (Gampe et al., 2015) and declines in the elderly (Diersch et al., 2012). This decline is associated with differences in activation patterns in the sensorimotor system between younger and older participants (Diersch et al., 2013; Diersch, Jones, & Cross, 2016). In sum, while studies on motor experience indicate a linear increase of action perception with age, previous work on action production skills suggests a more inverted U-shaped trajectory of action perception across the life span.

Along with these life long changes in motor experience and action production skill, advancing age is associated with variations in other factors. In infancy and childhood, social and emotional skills (Bukowski, Laursen, & Rubin, 2009) as well as cognitive abilities (Kochanska, Coy, & Murray, 2001) develop and children become more proficient in the according tasks (Zelazo, Müller, Frye, & Marcowitch, 2003). In late adulthood, increasing age is accompanied by a decrease in cognitive functioning (e.g., working memory capacity or executive functions; Salthouse, 2005, 2009), poorer health (Leist, Kulmala, & Nyqvist, 2014), changes in social networks (Holmén & Furukawa, 2002) and differences in emotion regulation (Brassen, Gamer, Peters, Gluth, & Buchel, 2012). All of these factors might contribute differently to life-span variations in action perception, production, and their interrelation and a theoretical framework is needed to integrate different age-related influences. Therefore, we embed the present research in such a framework, the complex dynamic system approach (Thelen & Smith, 1994). This approach allows explaining and predicting age-related changes across the life span. The approach is centred around the idea that development unfolds in a dynamic and interactive way (Smith & Thelen, 2003). According to this dynamic system approach, life-span development can be understood as a multicausally determined self-organising process (Smith & Thelen, 2003). Observable behaviour results from the dynamic, nonlinear and real-time interaction of various components (e.g., language, memory) on different levels of hierarchy (e.g., neurons, tissues, cortical regions; Thelen & Smith, 1994). Changes in behaviour across development occur when one or more components of such a dynamic system change beyond a certain threshold. That is, while the system shifts from one relatively stable state to another, the interactions between components are destabilised and reorganised. Such phase transitions are characterised by instable states of the dynamic system (Thelen & Smith, 1994) and are more frequent towards the start and the end of the life span (Johnson, 2000; Park & Reuter-Lorenz, 2009).

In line with the principles of the complex dynamic system approach, the age-related and observable differences in action perception and production may be seen as the developmental output of the interaction between various components. These components may include factors within the domains of cognitive, emotional, social and motor development. Together, these components spontaneously organize themselves into a self-sustained state (attractor state). That is, cognitive, emotional, social, and motor components find a stable pattern in their individual characteristics and interactions with each other across hierarchy levels (Thelen & Smith, 1994; van Geert, 2011). This state is robust against perturbations and the system goes back to it when pushed out of it. On the behavioural level, the relative rigidity or flexibility of such a state can be approximated by measuring the amount of recurrence in participants' behaviour. Within a recurrence quantification analysis (RQA; Zbilut & Webber, 1992), patterns within any (nonlinear) behavioural time-series may be identified. Or put differently: By employing RQA on participants' behaviour across any time frame (i.e., ranging from milliseconds to years), one may explore whether the same behaviour re-occurs again indicating a more stable state of underlying dynamic system. Hence, this form of time-series analyses captures the complexity of behaviour and the dynamic system resulting in this behaviour. Within the current study, two factors were assumed to have a particularly strong impact on these dynamics of the system associated with observable action perception and production. As highlighted above, these two factors are the participants' age (as an approximation of their motor experience) and their action production skill.

In sum and based on the work reviewed so far, the interrelations of action perception and production can be expected to experience quite an amount of variability across individuals (of different ages). However, our knowledge on the action perception-production coupling is so far based on studies investigating selective age groups. Furthermore, some age groups (e.g., children, adolescents, middle-aged adults) have been neglected almost completely in previous work. Also, different measurement techniques (e.g., eye tracking, EEG, fMRI) and dependent variables (e.g., action anticipation, desynchronisation of the mu-rhythm, BOLD response) were employed. These issues make it difficult to compare findings across studies and age groups. Therefore, no coherent picture of the interrelations between action perception and action production across the life span is possible to this date. That is, it is not known whether action perception and production follow the same life-span trajectory or whether their coupling is influenced by age-related influences as well. The current study was designed to fill this gap in research. To capture such a life-long trajectory, eye tracking was used as measurement technique because it is suitable for children and adults likewise. The study was furthermore embedded in the theoretical framework of the dynamic system approach to account for the dynamics of the interrelation between action perception and action production from a life-span perspective.

Using eye tracking, we assessed eye movements of participants between 3 and 80 years during action observation. We adapted a paradigm from Gampe et al. (2015), which has previously been used with toddlers aged 12 to 30 months. This was done to make sure that all participants were able to full-fill the task demands. Furthermore, the results of the original study indicated variance in toddler's performance and a potential for it to improve further. Within this paradigm, the toddlers observed two manual multi-step actions in which blocks were moved into a box using a tool. The manual movements and the tools differed in their familiarity between the two actions (*familiar* and *unfamiliar* condition). Specifically, the action in the unfamiliar condition was less transparent in its affordance than the action in the familiar condition and consisted of a novel combination of familiar action steps. After observing the action (*action-perception task*), participants were asked to reproduce the observed action with the same objects at their disposal (*action-production task*). The participants' action production skill was assessed via the accuracy of their imitation of the previously observed actions. The findings of the original study indicated a difference in action perception and action production between the two actions with an advantage for the familiar action.

In the current study, action production skill was measured via imitation accuracy similarly to the original study. This measure of action production has been used previously in childhood (Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012; Sommerville et al., 2005) and adult samples (Casile & Giese, 2006). Furthermore, we included and compared two measures of action perception in the current study. As a more traditional measure of action perception, we calculated the frequency of predictive eye movements to the action goal. Predictive gaze shifts are used to measure action perception in children as well as adults (Falck-Ytter et al., 2006; Flanagan & Johansson, 2003; Gesierich, Bruzzo, Ottoboni, & Finos, 2008; Melzer et al., 2012). Specifically, Flanagan and Johansson (2003) showed that these predictive eye movements are present during both production and perception of simple goal-directed actions. Similarly, Rosander and von Hofsten (2011) showed that this coupling between gaze and hand movement is already present in 10-month-olds. Furthermore, predictive eye movements are causally related to the recruitment of the observer's motor system during action perception (Elsner, D'Ausilio, Gredebäck, Falck-Ytter, & Fadiga, 2013) and facilitated by prior motor experience (Cannon et al., 2012).

However, oculomotor abilities change across the life span (Pratt, Dodd, & Welsh, 2006). For instance, when comparing infants gaze behaviour to those of adults within an action prediction paradigm, the infants made more saccades to reach the action goal and consistently arrived at the action goal later than the adults (Rosander & von Hofsten, 2011). Similarly, in saccadic reaction time paradigms, older adults show longer latencies when initiating a saccade

(Pratt et al., 2006) and longer saccade duration (Munoz, Broughton, Goldring, & Armstrong, 1998) compared to younger adults. Therefore, action perception as operationalized via age-sensitive measures such as (gaze) latencies may not easily be compared between children and adults. That is, since the anticipation of an action is influenced by how fast one is able to initiate and perform a saccade, traditional measures of action perception such as anticipation frequency and latency may be biased when measured across different age groups. A more idiosyncratic measure of action perception is the characterisation of gaze behaviour time-series. By employing recurrence analysis (as one of many possible analysis techniques of behavioural time-series) on the participants' gaze behaviour, we explored the relative stability of participants' gaze behaviour as a more covert measure of action perception. One main advantage of the RQA for the current study is that it depends less on participants' age-related oculomotor abilities. In contrast to the analysis of anticipation frequencies, where the time point and the location of a predictive fixation is determined by the researcher, the RQA analyses patterns in gaze behaviour with less of such presumptions. Within our recurrence analysis, we investigated whether certain states in gaze behaviour recur (i.e., whether participants re-fixate previously fixated areas on screen) while observing the two different multi-step actions as a reference of the dynamic system's stability (*recurrence*; Anderson, Bischof, Laidlaw, Risko, & Kingstone, 2013). In particular, we were interested how this stability changes with respect to age and action production skill. Previous research has shown that participants' action production skill was associated with the recurrence in their gaze during action perception (Vaidyanathan, Pelz, Alm, Shi, & Haake, 2014). Hereby, higher recurrence rates in participants' gaze behaviour (i.e., more re-fixations of certain screen areas) indicate higher stability and less flexibility in the dynamic system (illustrations of high and low recurrence in Figure 2).

Taken together, the current study investigates the influence of the skill to produce a specific action on the perception of familiar and unfamiliar actions across the life span. Based on previous findings (Adolph & Berger, 2011; Kauranen & Vanharanta, 1996), we expected the accuracy of participants' action production to follow an inverted U-shaped trajectory across life span. When looking at action perception, we did not expect to find a substantial influence of age or action production skill on the perception of the familiar action, since this action has been shown to already be familiar to children of 12-30 months of age in the original study (Gampe et al., 2015). In contrast, with respect to the unfamiliar action, we assumed participants' action perception as indicated by anticipation frequencies to either increase linearly with advancing age or to follow an inverted U-shaped trajectory. That is, because participants accumulate motor experience across their life span, this could be associated with a paralleled increase in action perception. Or put in other words: With increasing age it is more likely that certain action steps of the unfamiliar action have been produced and perceived before. That is, unfamiliar actions become more and more familiar with age. Alternatively, their action perception is influenced by action production skills therefore follows a similar U-shaped trajectory. Moreover, we assumed gaze patterns to be less recurrent towards the upper and lower end of the life trajectory as an indicator of destabilisations within the dynamic system in young children and older adults (Thelen & Smith, 1994).

## Methods

### Participants

In the current study, $N = 214$ participants evenly distributed across the ages of 3 to 80 years were included (Table 1). We aimed at doubling the sample size per age group of the original within-subject study (~ 15 participants per age group; Gampe et al., 2015) since we were to conduct between-subject analyses. We measured the behaviour of children between 3 and 4 years and 8 and 10 years as well as adolescents between 14 and 16 years and adults between 20 and 80 years into the study. The spacing between age groups was closer in childhood compared to adulthood because we expected changes to manifest themselves faster in younger years (Li et al., 2004). The three childhood samples were equally spaced to exemplarily measure across a larger part of childhood. All adult participants reported normal or corrected-to-normal vision and above-average general health according to the RAND 36-Item Health Survey (Hays, Sherbourne, & Mazel, 1993).

Table 1

*Participant Characteristics*

| | Familiar Condition | | | Unfamiliar Condition | | |
|---|---|---|---|---|---|---|
| Age (years) | *N* | % female | Handedness | *N* | % female | Handedness |
| 3-4 | 14 | 43 | 80.77(13.20) | 14 | 43 | 77.50(32.51) |
| 8-10 | 14 | 38 | 85.38(31.52) | 12 | 58 | 90.83(11.65) |
| 14-16 | 8 | 63 | 80.00(17.73) | 9 | 56 | 82.22(16.41) |
| 20-29 | 15 | 67 | 52.35(57.04) | 17 | 65 | 39.65(54.53) |
| 30-39 | 13 | 85 | 76.25(41.81) | 12 | 58 | 43.02(66.14) |
| 40-49 | 8 | 50 | 83.33(35.63) | 8 | 25 | 91.25(21.00) |
| 50-59 | 11 | 73 | 56.52(52.25) | 12 | 58 | 51.33(70.49) |
| 60-69 | 15 | 60 | 74.73(50.31) | 14 | 57 | 79.29(32.95) |
| 70-80 | 9 | 44 | 66.37(53.24) | 9 | 56 | 74.96(59.89) |

*Note.* Sample size, gender and handedness are reported for the two experimental conditions separately (between-subject design). Handedness (in % right; *M* (*SD*)) was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971) for ages 8 to 80. For the children between 3 to 4 years a behavioural adaption of the Oldfield Inventory (i.e., children were asked to perform the according actions) was used and children's handedness was coded from video.

All procedures were approved by the local research committee of the University of Zurich and performed in accordance with the ethical standards of the 1964 Helsinki declaration and its later amendments. Participants or their parents (for children until 16 years of age) gave written informed consent. The adults were recruited via mailing lists and public announcements. They received a reward of an approximate value of USD 15 for their participation. Children up to 10 years were recruited from a database of parents who had volunteered to participate in developmental studies with their children. They received a gift worth approximately USD 5 after their participation; no financial compensation was given to the parents. Children between 14 and 16 years were recruited via birth records and were given a cinema voucher (value of approximately USD 15) for their participation. The participants of this study are an age-matched subset of a larger sample to ensure an even distribution of participants across both experimental conditions.

**Materials**

The materials were adapted from Gampe et al. (2015). In the action-perception task, participants were presented with video recordings of two actions varying in familiarity to the observer (*familiar* and *unfamiliar* condition). In both conditions, the goal of the action was to put four different coloured blocks into the according holes in a box of the same colour using a tool. The boxes (visual angle: 16.1 x 8.1 x 6.5°), blocks, and tools were similar in form and size across the two conditions. However, the two conditions differed in colour of the boxes and blocks as well as type of tool used. While a hammer was used in the familiar condition, the tool in the unfamiliar condition consisted of a lever with a Velcro-covered end that could be attached to a Velcro-covered lever at the box (see Figure 1 for an overview of the materials and actions).

Hence, while the overall goal for both conditions was the same, movements and tools used to achieve the goal differed. Specifically, in familiar condition the blocks were placed on the box on a straight movement path and then hammered into the box. In the unfamiliar condition, the blocks were placed on the box using a rotating end-state comfort movement (i.e., block was grasp with the left hand and rotated during transportation) and an unfamiliar lever tool was used to insert them into the box. Each video comprised four action sequences, one sequence for each of the coloured blocks. Each action sequence consisted of four action steps: The block was grasped (Step 1), transported and placed on top of the box (Step 2), the tool was grasped (Step 3), and the block was entered into the box using the tool (Step 4). The action sequences for each of the four blocks were later edited to equal length. However, the length of the two conditions differed due to the natural variation in movement (for exact timing see Gampe et al., 2015). The participant's eye movements were measured using an Eyelink 1000Plus near infrared eye-tracker (SR Research, Canada, sampling rate: 500 Hz) and the stimuli were presented using the software Experiment Builder Software (SR Research). A 9-point calibration was used for the adults and a 5-point calibration was used for the children. Stimuli were presented on a 17" display. The display as well as the near-infrared lights and the camera were mounted on a movable arm in 60 cm distance to the participant.

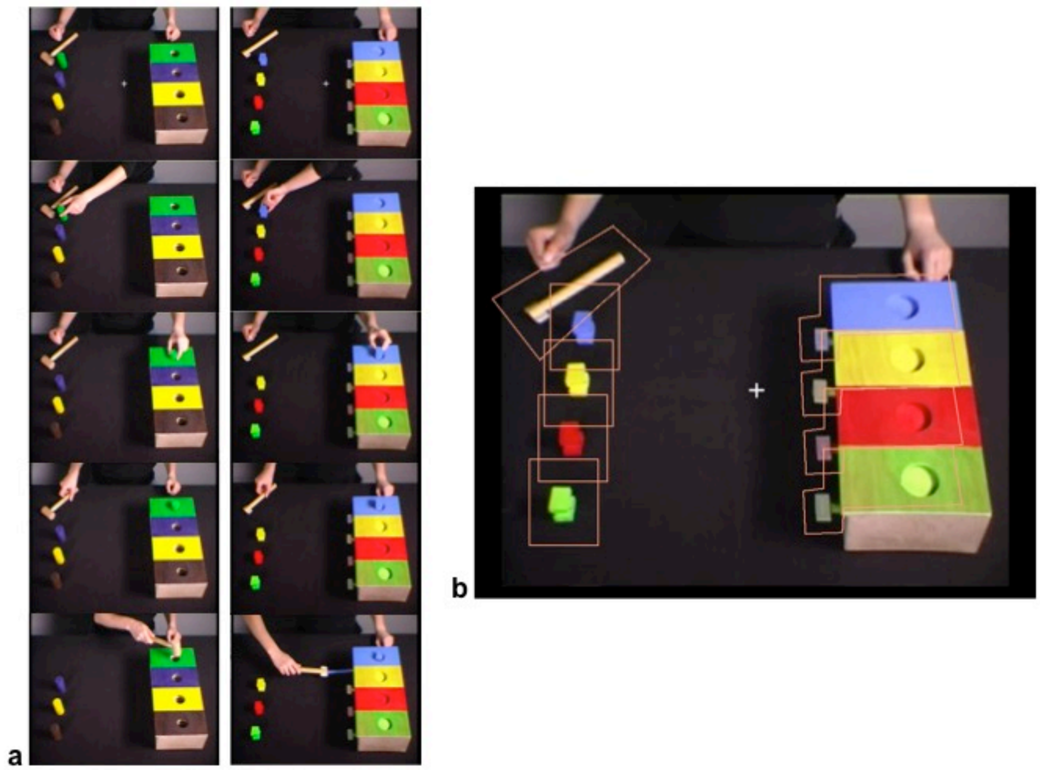


*Figure 1*. a. Action sequences of the two actions (familiar and unfamiliar). b. The areas of interest (AOIs) were similar to Gampe et al. ( 2015) and consisted of the action goals of each action step.

**Design and procedure**

The procedure was held as constant as possible for all age groups. Two exceptions were inevitable. First, for the children (3 to 16 years), the experimental session was preceded by a short familiarisation and instruction phase in the lab's playroom as well as a handedness test. Second, because the adults were tested within a larger project, they had already completed a number of eye-tracking tasks before engaging in the one described in this study (depending on order: 3 to 6 tasks in 10-30 minutes).

The two conditions were presented in a counterbalanced order. Within each condition, the videos showing the actions were shown three times to the participating children and two times to the adult participants. This was done to ensure that the children had enough opportunities to learn the action sequence for the proceeding action-production task (similar to Gampe et al., 2015). However, adult pilot data suggested transfer effects from one condition to the other (e.g., increases in anticipation frequencies in the second compared to the first condition observed), probably because both actions follow a similar structure. Therefore, and to compare action perception across children and adults, only the first two videos of the first condition presented to every participant were analysed. All further analyses are based on between-subject data. In each condition, the observation of the action recordings was followed by the action-production task of the respective action. The participants were instructed to reproduce the observed action as accurate and as fast as possible with the original materials. Participants' performance in the action-production task was video-recorded.

**Data analysis**

**Action-perception task.** The eye-tracking data was processed with the software Data Viewer (SR Research). The areas of interest (AOIs) were similar to Gampe et al. (2015) and consisted of the action goals of each action step (see Figure 1 for a spatial overlay with the materials presented). For Step 1 the action goals were the blocks (AOI area: 22.3°), for Step 2 and 4 the action goals were the coloured areas on top of the box (AOI area: 34.5°), and for Step 3 the action goals were the two tools (AOI area: 34.3°). If participants' gaze was located in two AOIs at the same time, the goal AOI of the current action step was given priority. Since non-overlapping AOIs are a prerequisite for the recurrence analysis (as described below), the AOI surface was reduced to the surface of the goal objects for this analysis.

***Anticipation frequencies.*** To obtain the frequency of anticipatory gaze shifts towards the action goal, the difference in time between the arrival of the actor's hand in the respective goal AOI and the participant's first fixation in the same area was calculated (gaze latency) for every action step. To ensure sufficient data quality, only action steps were included in which participants provided valid data for at least half of the total action step duration (*M* = 75.00%, *SD* = 0.80 of all trials). Next, for each participant, the number of action steps in which the participant's gaze arrived prior to the actor (predictive gaze shift) were divided by the total number of action steps that passed the quality criterion (predictive and reactive gaze shifts) resulting in an average individual anticipation frequency.

***Recurrence analysis.*** Recurrence analyses have been used previously to describe complex dynamic systems (e.g., climatological data: Marwan & Kurths, 2002; heart-rate variability: Marwan, Wessel, Meyerfeldt, & Schirdewan, 2002), and to analyse gaze patterns (Anderson, Anderson, Kingstone, & Bischof, 2015; Anderson et al., 2013). Within our recurrence analysis, we analysed the participants' fixations across the AOIs in intervals of 500 ms across the first two videos observed. That is, for each interval we assessed whether the participants' eyes were located within one of the goal AOIs (as described above) or within the rest of the display at this point in time. This resulted in a fixation sequence across nine goal AOIs and one non-goal AOI (e.g., 0-500 ms: AOI 1, 500-1000 ms: AOI 3, 1000-1500 ms: AOI 9 etc.). The sequence of fixations across the goal areas only (as indicated via the according AOIs) was then entered into a recurrence analysis (RQA; Zbilut & Webber, 1992) performed with R (R Core Team, 2012). Therefore, the analysis included fixations in AOIs independent of the current location of the currently performed action.

Within recurrence analysis, two fixations are considered recurrent if they are close together. In our study, this closeness was defined via the areas of interest. Hence, we considered fixations to be recurrent if they land in the same AOI. The recurrence rate is defined as the percentage of recurrent fixations per fixation sequence. It indicates how often observers re-fixated previously fixated AOIs and whether certain states of the system recurred over time as a reference of the stability of the system. In short, higher recurrence is associated with a more stable state of the dynamic system. Recurrence is usually illustrated with recurrence plots (Figure 2). Within these plots, the fixation sequence is plotted with itself over all intervals and re-occurring fixations are represented with recurrent points.

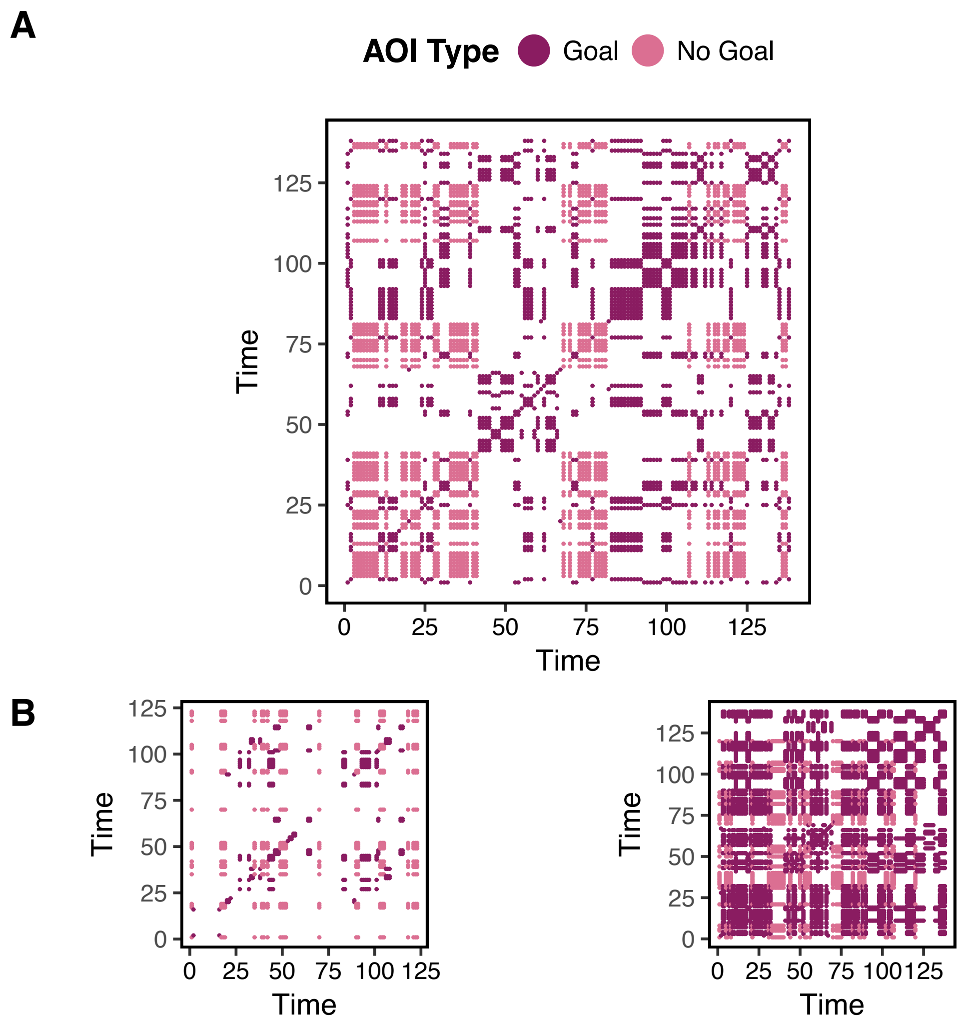


*Figure 2*. Recurrence is illustrated with recurrence plots. In these plots, recurrence of a fixation sequence is plotted with itself over all possible time intervals. The three recurrence plots shown here represent data of three individuals of different ages and of different conditions. Please note that time is represented as the number of time intervals (each 500 ms). If a participant fixates a certain AOI in time interval x and re-fixates the same AOI in time interval y, then a recurrence point is drawn at coordinate (x, y). A: Darker recurrence points represent recurrent fixations within the goal AOI's, lighter recurrence points represent fixations within the rest of the display. We measured the number of darker recurrence points as a proportion of all recurrence points (recurrence rate (RR) = 0.12). B: Examples of recurrence plots showing low (RR = 0.02; left) and high (RR = 0.23; right) recurrence as indicated by the number of darker recurrence points.

**Action-production task.** Performance in the action-production task was coded from video by three different trained coders (κ > .85). For every action step, participants' imitation was compared to the actions presented during the perception task. Actions steps were considered correctly reproduced if they were executed with the correct hand (right hand for block grasp and left hand for tool grasp), if the blocks were transported towards the box on the same movement path (straight in the familiar condition and rotational in the unfamiliar condition), if the colours of the blocks and the box segment matched up, and if the according tools were used to enter the blocks into the boxes. Every multistep action consisted of four action sequences à four action steps. Therefore, the participants' imitation score could take a number between 0 and 16. The imitation score of $n = 2$ participants in the familiar condition, and $n = 2$ participants in the unfamiliar condition could not be obtained because of technical problems with the video-recording system.

## Results

The results section is divided into three sections. First, we will present the results on the relation of age and action production skill. Second, the association between age and action perception is reported. Within the third section, the data on the interrelation of action perception and action production skill across the life span are presented. In all sections, action perception is operationalized by the anticipation frequencies as a measure of overt behaviour and by recurrence as a measure of covert behaviour. To make scales comparable, all independent variables were z-standardised before being entered into the analysis (see Appendix A1 for zero-order correlations of all variables of interest).

**Age and action production skill**

Using R (R Core Team, 2012), two polynomial regressions were conducted to analyse the effect of age on imitation score within each condition separately (Figure 3). For the familiar condition, results show significant linear (β = 0.079, *SE* = 0.013, $p < .001$) and quadratic effects of age (β = -0.003, *SE* = 0.001, $p < .001$). This indicates that participants action production skill followed an inverted U-shaped form across the life span, $F(2,102) = 25.330$, $p < .001$, $R^2 = .332$, indicating a more precise action production in young and middle-aged adults compared to young children and old adults. The same results pattern was found for the unfamiliar condition, $F(2,102) = 14.410$, $p < .001$, $R^2 = .220$. Again, the results yielded a significant linear (β = 0.052, *SE* = 0.012, $p < .001$) and a significant quadratic association of age and imitation score following the same inverted U-shaped pattern as reported before (β = -0.003, *SE* = 0.001, $p < .001$; Figure 3 and Appendix A2).

**Age and action perception**

**Anticipation frequency.** We conducted two separate linear regressions of age on the anticipation frequencies in the two conditions (Figure 3). In the familiar condition, age was not associated with the participants' anticipation frequency, $F(1,105) = 0.362$, $p = .549$. In the unfamiliar condition, the more parsimonious linear model, $F(1,105) = 7.153$, $p = .009$, $R^2 = .064$, yielded the same fit ($p = .129$) with the data like a quadratic model, $F(2,104) = 4.793$, $p = .010$, $R^2 = .084$. Accordingly, the linear model was employed, which indicated that in the unfamiliar condition, participants predicted more action steps with increasing age (β = 0.002, *SE* = 0.001, $p = .009$; see Appendix A3 for details of regression analyses).

**Recurrence.** Two linear regression analyses of age on recurrence were conducted for each condition separately (Figure 3). The results show no effect of age on the recurrence in the familiar condition, $F(1,105) = 1.083$, $p = .300$. In the unfamiliar condition, a linear model,

$F(1,105) = 2.332$, $p = .130$, fit the data less ($p = .003$) than a quadratic model, $F(2,104) = 5.878$, $p = .004$, $R^2 = .102$. That is, fixations were less recurrent in young children and in older adults compared to adolescents, young and middle-aged adults (linear: $\beta < 0.001$, $SE < 0.001$, $p = .014$; quadratic: $\beta < -0.001$, $SE < 0.001$, $p = .003$; see Appendix A3 for details of regression analyses).

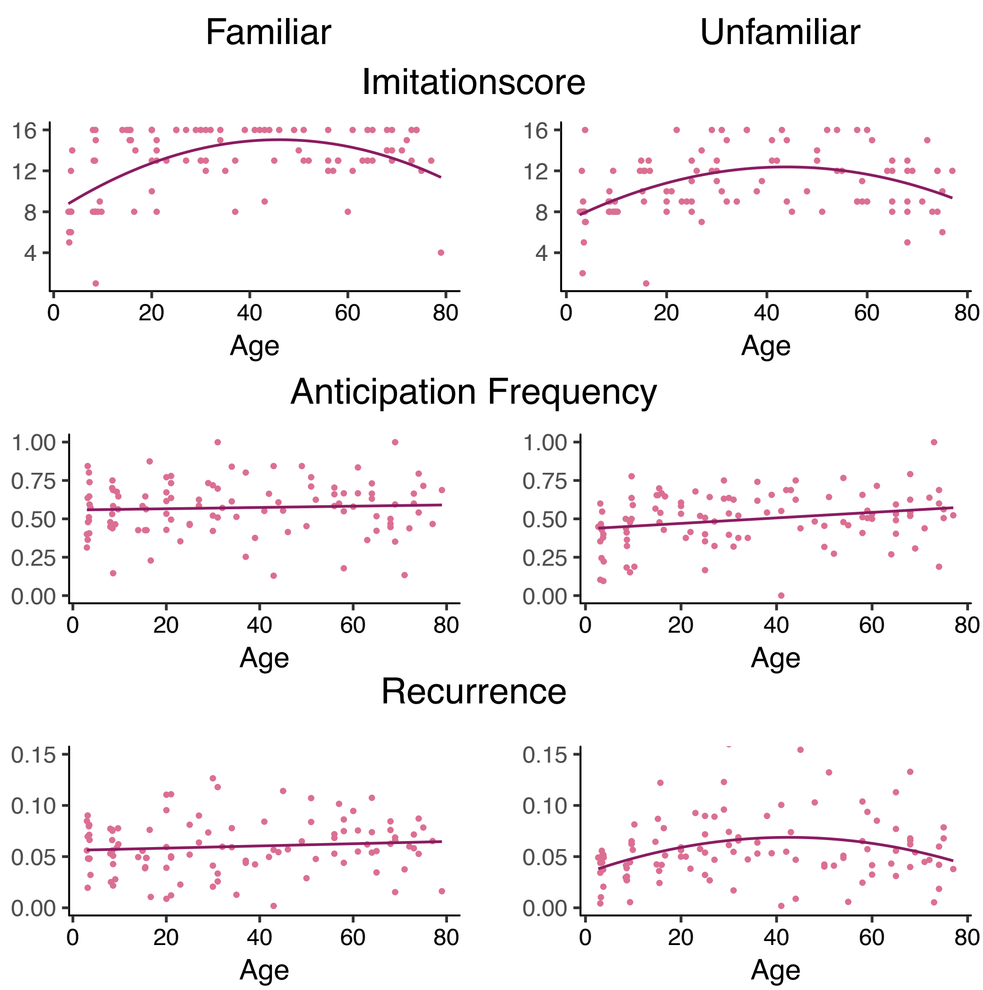


*Figure 3*. Relationship between age and imitation score, anticipation frequency and recurrence for the familiar (left) and the unfamiliar action (right).

**Action production skill and action perception across the life span**

**Anticipation frequency.** For each condition, we explored the association of participants' imitation score and their anticipation frequency and investigated whether age moderates this relationship. Two linear regressions with imitation score, age, and their interaction on anticipation frequency were conducted. In the familiar condition, the results showed no associations between imitation score and anticipation frequency, $F(3,101) = 0.209$, $p = .890$. In the unfamiliar condition, the regression model, $F(3,101) = 2.761$, $p = .046$, $R^2 = .076$, yielded no significant association of imitation score with anticipation frequency ($\beta = 0.001$, $SE = 0.005$, $p = .848$). Furthermore, a significant effect of age ($\beta = 0.002$, $SE = 0.001$ $p = .008$) but no interaction between imitation score and age ($\beta < 0.001$, $SE < 0.001$, $p = .750$) emerged. Hence, older participants predicted action steps of the unfamiliar action more frequently than younger participants independent of their imitation score (see Appendix A4 for details of regression analyses).

**Recurrence.** Similarly, the association of participants' imitation score and recurrence as well as a possible moderating effect of age were explored for the two conditions separately. Two separate regressions of age and imitation score, and their interaction on recurrence were conducted. In the familiar condition, the results show showed no significant associations, $F(3,101) = 1.208$, $p = .311$. However, in the unfamiliar condition, a quadratic model, $F(5,99) = 4.722$, $p < .001$, $R^2 = .193$, indicated a significant linear association of imitation score ($\beta = -0.003$, $SE = 0.001$, $p = .041$), as well as a linear ($\beta < 0.001$, $SE < 0.001$, $p = .010$), and a quadratic association of age ($\beta < -0.001$, $SE < 0.001$, $p < .001$) with recurrence. No interaction between imitation score and age emerged (linear: $\beta < -0.001$, $SE < 0.001$, $p = .055$; quadratic: $\beta < 0.001$, $SE < 0.001$, $p = .814$). Hence, in the unfamiliar condition, high imitation scores were related to less recurrent gaze behaviour independent of age (see Appendix A4 for details of regression analyses).

## Discussion

The current study investigated the association between individual's particular capability to produce a specific action and their perception of goal-directed actions across the life span. To this end, participants from 3 to 80 years observed a familiar or an unfamiliar action and thereupon were asked to imitate the according action. Action perception was measured via the participant's prediction of the action goal and the recurrence of their gaze behaviour during the observation of the actions. Action production skill was measured via the closeness of participant's imitation of the observed action. The results showed no relationship between age and action perception – measured via anticipation frequency and recurrence – in the familiar condition. Similarly, the participants' action production skill was not associated with their action perception for the familiar action. In contrast, when observing unfamiliar actions, anticipation frequencies linearly increased with age. Furthermore, participants' gaze behaviour was less recurrent, that is, more variable at both ends of the age spectrum in the unfamiliar condition. When looking at relationship of action production skill and action perception across the life span, no association was found for anticipation frequencies. However, participants with a high imitation score were less recurrent in their gaze behaviour in the unfamiliar condition across the life span. In sum, our results indicate that action perception differs across the life span. These differences vary with the familiarity of the action to the observer and his or her accuracy in imitating the according action. In the next paragraphs, we will discuss the life-span trajectories of these interrelations separately for our two measures of action perception applied (anticipation frequency and recurrence).

**Anticipation frequency across the life span**

Anticipation frequency linearly increased with age for the unfamiliar action. This is in line with previous studies suggesting that life-long, accumulated motor experience changes how actions – produced or perceived – are processed (Diersch et al., 2013; Falck-Ytter et al., 2006; Knoblich & Flach, 2001; Loucks & Sommerville, 2012; Melzer et al., 2012). However, studies with both infant and adult participants (Cross, Hamilton, & Grafton, 2006; van Elk et al., 2008) also showed that it takes a considerable amount of motor experience with a certain action before this has an impact on action perception. In line with this, we still found an increase of anticipation frequency with advancing age in the unfamiliar condition while there was no effect of age in the familiar condition. Hence, while the familiar action was already familiar enough to the youngest participants to be anticipated with a relatively high frequency, the accumulated action experience over age was beneficial when it came to predicting the action goals of the unfamiliar action. This is in line with previous studies indicating a change in sensorimotor activity during action observation before and after motor experience with the according action (Gardner, Aglinskas, & Cross, 2017; Gardner, Goulden, & Cross, 2015).

**Recurrence across the life span**

Similar to our findings on anticipation frequencies, participants' age affected recurrence only in the unfamiliar, but not in the familiar condition. The analysis of the time-series of participant's gaze behaviour allows capturing the complexity of dynamical systems such as life-span development in more detail than the relatively rough measure of anticipation frequencies. Recurrent fixations are associated with recognition and the availability of an internal action representation (Noton & Stark, 1971). The re-fixation of previously fixated areas on the screen can be interpreted as a reassurance of the correctness of this representation and the predictions that can be derived from this representation. Furthermore, recurrence quantification analysis gives insights into process factors. It approximates the relative stability or instability of the underlying system. More stable phases of dynamic systems are accompanied with increased predictability of behaviour (as indicated by high recurrence rates), while reorganizational processes within the system during instable phases (as indicated by low recurrence rates) lead to less predictable and highly variable behaviour (Thelen & Smith, 1994). In the current study, the participants' gaze behaviour was less recurrent at the two ends of the age spectrum within the unfamiliar condition – indicating less stable states. Therefore, we assume the development of action perception to undergo periods of transition in childhood, stabilisation in adulthood and destabilisation later in life, which are observable in the differences in the recurrence in gaze behaviour.

This assumption finds support in other theoretical frameworks on life span development. For instance, the interactive specialization approach (Johnson, 2000, 2001) assumes neural structures to be activated via multiple pathways and different stimuli in early phases of development. Through dynamic changes on the structural and functional level of cortical networks (e.g., pruning or inhibition of unused associations) these response properties become more specialized and cortical regions more selectively activated by certain kinds of stimuli. On the other end of the life span, the Scaffolding Theory of Aging and Cognition (STAC; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014) states that the brain seeks to maintain a delicate equilibrium while facing external (e.g., unfamiliar situations) and internal (e.g., aging) changes. This equilibrium is established through a constant reorganisation of the brain (e.g., strengthening of existing pathways, establishing new pathways or inhibiting ineffective connections). Together, these lines of thinking assume a dynamic and flexible cortical organisation across development and predict an increasingly narrower response pattern with increasing age during childhood and an again broadening of response patterns towards late adulthood.

**The interrelation between action perception and action production skill across the life span**

In contrast to previous studies (Ambrosini et al., 2011; Kirsch & Cross, 2015), the accuracy of action production was not associated with action perception as indicated by anticipation frequency (for both actions). We suggest, that the assessment of action perception via the frequency of predictive eye movements might be a too global measure not sensitive enough to capture subtle developmental processes (Thelen & Smith, 1994). In line with this, the findings show an association of action production with action perception measured via the recurrence in participants' fixation sequences (as more covert measure of action perception). However, this relationship was only found for the unfamiliar condition and we did not find an effect of action production skill on the recurrence in the familiar condition. This is probably because the dynamic system already resided in a relatively stable state for the perception of familiar actions, differences in one subcomponent such as the accuracy in producing the action may not elicit an observable effect. In contrast, the recurrence of the participants' fixation sequence did show a significant association with the imitation score for unfamiliar action: Participants with higher imitation scores showed lower recurrence in their gaze behaviour. While this might seem surprising at first sight, one has to keep in mind that we measured the recurrence of fixations within the goal AOIs. Learning a new action involves monitoring the scene and paying close attention to the exact kinematics of the movements used to reach the action goal (Hayes, Roberts, Elliott, & Bennett, 2014; Sumanapala, Fish, Jones, & Cross, 2017). That is, to successfully reproduce the observed actions, the participants had to look at areas on the screen that were not captured by the goal AOIs. Therefore, the recurrence of the fixation sequence within the action goal AOIs is likely to be negatively associated with the accuracy of action production. An alternative explanation of this finding is that the reduced recurrence in association with more accurate imitation indicates learning and flexibility within the dynamic system (Smith & Thelen, 2003). Specifically, a lower recurrence rate might not only be an indicator of transition phases, but the instability and reorganizational processes within the complex dynamic system represent adaptation to a new situation resulting in a behavioural output, which is closer to the observed action (van Geert, 2011; van Geert & Steenbeek, 2005).

Another possibility is that finding of a negative association between recurrence in participants gaze behaviour and their imitation accuracy might indicate a decoupling of action perception and action production in older adults (Costello & Bloesch, 2017; Kuehn et al., 2017). That is, older and younger adults are shown to weight incoming information differently when perceiving and producing actions. While children rely strongly on motor information, older adults focus more on visual information (Diaconescu, Hasher, & McIntosh, 2013; Frick, Daum, Wilson, & Wilkening, 2009; Mahoney, Verghese, Dumas, Wang, & Holtzer, 2012). This emphasis of visual over motor information is adaptive for older individuals since advancing age is associated with less distinct sensory input and dedifferentiation processes within the sensorimotor system (Bernard & Seidler, 2012; Heuninckx, Wenderoth, & Swinnen, 2010; Koppelmans, Hirsiger, Mérillat, & Seidler, 2015). Specifically, along with the changes in action production skill described in the introduction (Reuter et al., 2015; Seidler & Stelmach, 1995), older adults show decreases in the sensitivity of vision (Owsley, 2011), in motion perception as well as visual discrimination ability (Kuehn et al., 2017). Nevertheless, the described shift in focus from motor to visual information across the life span might influence the dynamics within the complex system and result in a decoupling of action perception and production in later adulthood (Costello et al., 2014; Costello & Bloesch, 2017). In line with this, older adults also recruit hippocampal areas during action perception, indicating more top-down influences of memory processes

(Diersch et al., 2013). Future research will have to explore, whether there is such a divergence in the overlapping processing of action perception and production in older adults.

The exploration of life span development has to be based on theoretical frameworks and measurement techniques, which are suitable for various age groups. The current study addressed these two issues by employing time-series analyses on gaze data and describing life-span development within a dynamic system approach (Thelen & Smith, 1994). This approach makes comparable predictions to other developmental frameworks such as the interactive specialization approach (Johnson, 2000, 2001) and the STAC (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014) and accounts for developmental processes across the whole life span. Moreover, the use of eye-tracking technology and the analysis of gaze time series seem to be a promising route in future life-span research since it gives insights in more covert processes. However, our study was based on cross-sectional data. We did not describe life-span development but only reported differences between age groups instead. Therefore, longitudinal studies are needed to give an appropriate picture of age-related influences on action perception.

With this study, we showed that action production skills are associated with action perception across the life span. Our results suggest that the development of the interrelations of action perception and production is to be seen within a dynamic system framework and does not follow linear pathways.

**Compliance with ethical standards**

All authors declare that they have no conflict of interest. All procedures were in accordance with the ethical standards of the institutional research committee and with the 1964 Helsinki declaration and its later amendments. Informed consent was obtained from all individual participants or their parents (for children until 16 years of age) included in the study.

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## Appendix A

Table A1

*Correlations among Variables of Interest*

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| Age (1) | - | .059 | .101 | .038 | .253** | .147 | .252** |
| Anticipation frequency, familiar (2) | .059 | - | .263** | .061 | - | - | - |
| Recurrence, familiar (3) | .101 | .263** | - | .000 | - | - | - |
| Imitation score, familiar (4) | .038 | .061 | .000 | - | - | - | - |
| Anticipation frequency, unfamiliar (5) | .253** | - | - | - | - | .224* | .086 |
| Recurrence, unfamiliar(6) | .147 | - | - | - | .224* | - | -.090 |
| Imitation score, unfamiliar (7) | .252** | - | - | - | .086 | -.090 | - |

*Note.* Zero-order correlations of variables of interest (** $p < 0.01$; * $p < 0.05$). Please note that anticipation frequencies, recurrence rate and imitation scores for familiar and unfamiliar actions were derived from two different age-matched samples.

Table A2

*Regression Analyses: Age on Imitation Score*

| Model | β | *SE* | $\Delta R^2$ | *p* |
|---|---|---|---|---|
| | Familiar condition | | | |
| Linear Model | | | .144 | < .001 |
| Constant | 12.637 | 0.319 | | < .001 |
| Age | 0.056 | 0.013 | | < .001 |
| Quadratic Model | | | .332 | < .001 |
| Constant | 14.573 | 0.459 | | < .001 |
| Age | 0.079 | 0.013 | | < .001 |
| $Age^2$ | -0.003 | 0.001 | | < .001 |
| | Unfamiliar condition | | | |
| Linear Model | | | .063 | .010 |
| Constant | 10.601 | 0.300 | | < .001 |
| Age | 0.033 | 0.013 | | .010 |
| Quadratic Model | | | .220 | < .001 |
| Constant | 12.133 | 0.434 | | < .001 |
| Age | 0.052 | 0.012 | | < .001 |
| $Age^2$ | -0.003 | 0.001 | | < .001 |

Table A3

*Regression Analyses: Age on Measures of Action Perception*

| Model | β | *SE* | $\Delta R^2$ | *p* | β | *SE* | $\Delta R^2$ | *p* |
|---|---|---|---|---|---|---|---|---|
| | Familiar condition | | | | | | | |
| | Anticipation frequency | | | | Recurrence rate | | | |
| Linear Model | | | .003 | .549 | | | .010 | .300 |
| Constant | 0.572 | 0.017 | | < .001 | 0.060 | 0.000 | | < .001 |
| Age | 0.000 | 0.000 | | .549 | 0.000 | 0.000 | | .300 |
| Quadratic Model | | | .009 | .615 | | | .010 | .590 |
| Constant | 0.589 | 0.027 | | < .001 | 0.060 | 0.004 | | < .001 |
| Age | 0.000 | 0.000 | | .407 | 0.000 | 0.000 | | .330 |
| $Age^2$ | -0.000 | 0.000 | | .434 | -0.000 | 0.000 | | .990 |
| | Unfamiliar condition | | | | | | | |
| | Anticipation frequency | | | | Recurrence rate | | | |
| Linear Model | | | .064 | .009 | | | .022 | .130 |
| Constant | 0.496 | 0.016 | | < .001 | 0.057 | 0.003 | | < .001 |
| Age | 0.002 | 0.001 | | .009 | 0.000 | 0.000 | | .130 |
| Quadratic Model | | | .084 | .010 | | | .102 | .004 |
| Constant | 0.527 | 0.025 | | < .001 | 0.068 | 0.005 | | < .001 |
| Age | 0.002 | 0.000 | | .003 | 0.000 | 0.000 | | .014 |
| $Age^2$ | -0.000 | 0.000 | | .129 | -0.000 | 0.000 | | .003 |

Table A4

*Regression Analyses: Imitation Score on Measures of Action Perception*

| Model | β | *SE* | Δ$R^2$ | *p* | β | *SE* | Δ$R^2$ | *p* |
|---|---|---|---|---|---|---|---|---|
| | Familiar condition | | | | | | | |
| | Anticipation frequency | | | | Recurrence rate | | | |
| Model | | | .006 | .890 | | | .035 | .311 |
| Constant | 0.570 | 0.018 | | < .001 | 0.058 | 0.003 | | < .001 |
| Age | 0.000 | 0.001 | | .777 | 0.000 | 0.000 | | .154 |
| Imitation | 0.003 | 0.006 | | .549 | 0.000 | 0.001 | | .958 |
| Age * Imitation | 0.000 | 0.000 | | .667 | 0.000 | 0.000 | | .182 |
| | Unfamiliar condition | | | | | | | |
| | Anticipation frequency | | | | Recurrence rate | | | |
| Model | | | .076 | .046 | | | .193 | < .001 |
| Constant | 0.491 | 0.017 | | < .001 | 0.072 | 0.005 | | < .001 |
| Age | 0.002 | 0.001 | | .008 | 0.000 | 0.000 | | .010 |
| Age$^2$ | - | - | | - | -0.000 | 0.000 | | < .001 |
| Imitation | 0.001 | 0.005 | | .848 | -0.003 | 0.001 | | .041 |
| Age * Imitation | 0.000 | 0.000 | | .750 | -0.000 | 0.000 | | .055 |
| Age$^2$ * Imitation | - | - | | - | 0.000 | 0.000 | | .814 |